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Seasonality and community composition of springtails in Mexican forests

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ABSTRACT

Springtails or Collembola have wide distributions and occur at all latitudes and elevations, including at extreme environmental conditions. Some are associated with suspended soils, and others live in epiphytic plants, moss, lichens, bark crevices or on leaves and flowers. Their food resources are mainly vegetable matter and there are few predatory species. Springtails from the trees of Mexican forests have been studied, particularly those living in *Tillandsia* sp. (Bromeliaceae), but the canopy fauna has only recently been investigated with canopy fogging. These studies have showed that Collembola in the tropical canopy are the dominant arthropod group in abundance, in contrast to other geographical regions. The aims of the present study has been to compare the composition and communities of the springtails living in canopies of three different forest types in Mexico, and to analyse their seasonality. Specimens from central Mexico originated from epiphytic plants of the genus *Tillandsia*; other were obtained from fogging of a dry tropical forest on the Pacific coast and a tropical rainforest in Chiapas. The tropical dry forest was characterized by a high diversity of endemic and cosmopolitan species; most of them showing seasonal variation depending on humidity. There, 19 species of Collembola were collected; the most abundant and constant was *Salina banksi* (Paronellidae). The same species was very abundant in the tropical rainforest at Chajul. This species appears to be dominant in tropical Mexican forests, in contrast to the temperate forests in Hidalgo and Morelos states, where the most abundant species were *Sminthurinus quadrimaculatus* and *Pseudisotoma sensibilis*. There are important differences in composition between Collembola assemblages living in canopies and those of the soil and shrub layers. The structure of springtail assemblages varies significantly between seasons and forest types, depending on humidity and tree species.

INTRODUCTION

Since the nineteenth century, observations of arboricolous arthropods in tropical forests have been a major research focus in tropical biology (e.g. Bates, 1884). Technical considerations have almost always limited the study of these habitats, but the development of technologies for canopy access since the 1980s (Moffett & Lowman, 1995) has led to a rapid increase in analyses of the structure of arthropod assemblages (Erwin, 1995; Stork *et al.*, 1997a). These recent studies of natural forest canopies in temperate and tropical regions have showed that this habitat contains speciose, mostly unidentified and little-understood, associations of arthropods.

The fogging approach has been the most widely used research technique in recent years, presumably because of its simple design and practicality (Adis *et al.*, 1984; Watanabe & Ruaysoongnern, 1989; Stork, 1991; Guilbert *et al.*, 1995). This method was used in earlier studies conducted by Roberts (1973) to collect grasshoppers (Orthoptera) in Costa Rica. Since then, other researchers in different regions of the world have adopted and modified the approach.

Springtails or Collembola are usually associated with edaphic environments, where they are important for their sheer abundance and for the role that they play in nutrient cycling within the soil (Bardgett & Chan, 1999; Theenhaus *et al.*, 1999; Scheu & Falca, 2000). However, they can also be collected in great numbers from forest canopies (Palacios-Vargas *et al.*, 1998, 1999) and occupy various habitats, such as suspended soils (Delamare-Deboutevillc, 1948), epiphytic plants (Palacios-Vargas, 1981), moss, lichens, bark crevices (André, 1983), tree leaves and flowers. The role of

Collembola in the canopy can be as important as in the soil, particularly in sections of the canopy where large accumulations of organic matter occur. Distribution patterns of Collembola in the canopy vary spatially as well as temporally, and there is a strong vertical stratification stretching from the forest floor to the upper canopy (Rodgers & Kitching, 1998).

In this chapter, we present results of our studies and will compare the seasonal variations of the Collembola from the canopies of three different forests in Mexico: a tropical dry forest in Chamela, Jalisco; a tropical rainforest at Chajul, Chiapas; and a temperate *Quercus–Abies* forest in Central Mexico (Hidalgo and Morelos States).

METHODS

Study sites

Tropical dry forest, Chamela Biological Station

The Chamela region in Mexico is located on the coast of the State of Jalisco (19° 30′ N, 105° 03′ W), at 200 m above sea level (asl). It is limited in the north by the Sierra Madre del Sur, by the Pacific Ocean in the west, by the Transversal Neovolcanic system in the north-east and by Oaxaca State in the south (Bullock, 1988).

The region contains an ecological reserve of 3300 ha with a research centre run by the Universidad Nacional Autónoma de México. The dominant vegetation is tropical deciduous forest (Bullock, 1988). There are several small streams, and ephemeral rivers that flow during September (Cervantes, 1988). The slopes of the hillsides range mostly from 21° to 34° (Bullock, 1988). The soil includes sandy entisols of neutral pH and little organic matter (Solís, 1993b). The climate is Aw(x)i type: that is, warm subhumid with summer rains (Awx) but with low average rainfall and little thermal oscillation (less than 5 °C) occurring throughout the year (García, 1988). The average annual rainfall is 748 mm and 80% falls between July and October (Bullock, 1986). Hurricanes are frequent, resulting in erratic patterns of precipitation (García-Oliva *et al.*, 1991). The highest monthly average air temperatures (28.8–32.2 °C) occur from May to July, and the lowest monthly averages (15.9–22.6 °C) occur from December to February (Bullock, 1988).

The Station's flora consists of more than 780 species. The two families (among 107) of greatest diversity are the Leguminosae and Euphorbiaceae, followed by the Asteraceae, Convolvulaceae, Rubiaceae, Bromeliaceae, Malvaceae and Acanthaceae (Lott *et al.*, 1987). Trees reach a maximum height of 12 m and the main genera are *Lonchocarpus*, *Caesalpinia*, *Croton*, *Jatropha* and *Cordia* (Lott, 1985). These trees produce flowers and seeds when they lose their leaves, mainly during June and July (Bullock & Solís-Magallanes, 1990). There is a high diversity of epiphytes, mainly bromeliads of *Tillandsia* spp. (Lott *et al.*, 1987).

Tropical rainforest, Chajul tropical biology station

The station of Tropical Biology Chajul is 331 200 ha in area and is located in the southern end of the Montes Azules Biosphere Reservation (16° 4′–16° 57′ N, 90° 45′–91° 30′ W) in the north-eastern part of the State of Chiapas. The vegetation is mainly tropical rainforest (Gómez-Pompa & Dirzo, 1995). The climate is A(f)wi: warm and humid (Afw), more or less isothermal with an annual average temperature of over 22 °C, the average temperature being over 18 °C during the coolest month. Summers are rainy and affected by monsoon patterns, with annual precipitation reaching more than 2500 mm and up to 3000 mm in the most northerly part of the reserve.

The reserve is dominated by karst (limestone) relief patterns, with altitudes ranging from 300 to 1500 m. Lithosol soils prevail in the mountainous areas of the western part of the reserve. Because of their topographical characteristics, these soils are exposed to lixiviation, resulting in rather high soil acidity. More than 500 species of vascular plants have been recorded in the reserve (Rzedowski, 1988). Most of the reservation is covered by tropical rainforest, which ranges in altitude from 100 to 900 m asl. The highest trees reach 60 m and include the following species: *Terminalia amazonia* (J. F. Gmel.) Exell, *Lonchocarpus* sp., *Schizolobium parahybum* (Vell.) Blake, *Swietenia macrophylla* King and *Brosimum alicastrum* Swart.

Temperate Quercus–Abies *forest, 'El Chico' National Park and Chichinautzin lava flow*

The National Park El Chico is 2793 ha (Vargas Márquez, 1984) and is located on the north-eastern slope of the Valle de México (20° 13′ N, 98° 47′ W). The soil comprises mostly basaltic ashes, but andesitic and rhyolitic soils are also present. Organic matter is very high in the A horizon. Soil texture varies between sandy-clay and sand. Soils are for the most part quite deep and well drained (Aguilera, 1962). The climate of the area, as cited by García (1988) is a type Cb(m)(w)(i′)gw. This is temperate with long and fresh, humid summers and rainy winters. Annual average temperature ranges between 10 and 14 °C, with a minimum of −6 to −9 °C; annual rain averages between 600 and 1500 mm. The rainy season starts in May and continues through October to November. This period produces 80 to 90% of the annual precipitation, with the remainder falling during the winter and early spring (Melo & López, 1994).

The vegetation consists chiefly of forest dominated by *Abies religiosa* (H. B. K.) Schlecht. & Cham., standing between 20 and 30 m high. This forest is situated at elevations between 2700 and 3000 m, mainly on slopes where it is sheltered from strong winds and sun exposure. The *Quercus* forest occurs from 2300 to 3000 m in altitude and varies in appearance and composition. Dominant species include *Quercus laurina* Humb. & Blonpl., *Q. rugosa* Née, *Q. laeta* Liebm., *Q. mexicana* Humb. & Blonpl. and *Q. crassifolia* Humb. & Bonpl. Trees also reach heights of 20 to 30 m and support abundant epiphytic plants.

The Chichinautzin lava flow is located in Morelos State (19° 01′ N; 99° 09′ W) and occupies an area of approximately 300 ha. The altitude of the area varies between 2000 and 2650 m. In spite of its small area, two climate types are present in Chichinautzin: $C(W_2)(W)b(i')g$ at the northern end is one of the most humid of the temperate climates, with little variations in temperature (between 5 and 7 °C) through the year; and $(A)C(W_2)(W)ig$ at the southern end, which may be considered intermediate between tropical and temperate. Annual precipitation varies between 1236 mm at the southern end and 1608 mm in the northern part, and the temperature range is from 16.1 to 12.1 °C.

In the northern part, between 2450 and 2650 m asl, vegetation is dominated by *Q. rugosa*, whereas, between 2150 and 2450 m asl, an association of *Hechtia podantha* Mez. and *Agave horrida* Lemaire ex Jacobi is present, in addition to one of *Quercus–Arctostaphylos polifolia*. In the southern part, from 2000 to 2150 m asl, *Bursera cuneata* (Schl.) Engl. is common as are several *Tillandsia* spp. (Espinosa, 1962).

Springtail collections and statistical analyses

Insecticide knockdowns were performed in the three forest types to study the fauna of Collembola in their canopies. In Chamela Biological Station, a total of seven such sampling events were carried out from August 1992 to May 1994, a period including both the rainy season (August and September 1992, July 1993) and the dry season (May and November 1993, and February and May 1994). In the Chajul Tropical Biological Station, samples were taken during July 1994 and July 1995. At both sites, a fogging machine (Dynafog^{TM}) was used, releasing natural pyrethrum insecticide (3% resmethrin in a kerosene solution) about 30 minutes before sunrise (04:00 to 06:00). For each fumigation, a projected area of 100 m^2 was delimited and 50 funnels (0.5 m diameter) were hung randomly in the shrub layer about 50 cm above the forest floor. Specimens that fell into the funnels were then collected by washing them with alcohol (80%), up to 5 hours after fogging. Specimens from the temperate *Abies–Quercus* forest were obtained from two fogging collections performed by Tovar (1999) in February and August 1997. He also used a natural pyrethrum but in aqueous solution and fogged three isolated trees of six *Quercus* species (*Q. castanea* Née, *Q. crassifolia*, *Q. crassipes* Humb. & Bonpl., *Q. greegii* Trel., *Q. laeta* and *Q. rugosa*), setting 10 square collecting surfaces (0.99 m^2 in surface) under each tree. All specimens collected were stored in 70% alcohol. Collembola were mounted in Hoyer's solution and identified to species.

For statistical analysis, data were transformed as their square root ($\sqrt{(x + 0.5)}$) to satisfy the assumption of normality. Comparisons between seasons were performed with Student t-tests. To compare the effects of vegetation (three levels: rainy forest, deciduous forest and epiphytes) on springtail abundance an analysis of variance (ANOVA) was used, and *post hoc* comparisons were made using Tukey's test for unequal sample sizes. Species diversity in the four localities was compared with t-tests (Zar, 1974). Presence–absence data for Collembola genera were used to calculate levels of similarity among the four localities by cluster analysis, using unweighted pair-group average (UPGMA) as the gathering rule. Analyses were performed with the Statistica^{TM} Ver. 6 program (StatSoft, 1995).

RESULTS AND DISCUSSION

Assemblage composition of tropical dry forest at Chamela

At Chamela, 1 044 032 individuals (15 197 individuals m^{-2}) representing 19 species of Collembola were collected (Table 15.1). During the rainy season, Collembola represented 98% of the total canopy arthropods at Chamela, whereas in the dry season, they made up only 30% of the total (Fig. 15.1).

Salina banksi MacGillivray was the most abundant species, comprising 89.9% of all Collembola during

Table 15.1. *Average density of Collembola collected from the canopy at Chamela, Jalisco, Mexico and Student's* t*-test values for comparison between rainy and dry season*

Taxa	Average density (individuals m^{-2}) ±SD		
	Rainy season	Dry season	Student's t-test[a]
Hypogastruridae			
Ceratophysella gibbosa (Bagnall, 1940)	34 ± 56	3 ± 3	13.94*
Xenylla humicola (Fabricius, 1780)	76 ± 128	6 ± 9	13.12*
Brachystomellidae			
Brachystomella minimucronata Palacios-Vargas & Najt, 1981	26 ± 41	3 ± 5	13.82*
Neanuridae			
Neotropiella quinqueoculata (Denis, 1931)	31 ± 50	4 ± 5	11.07*
Pseudachorutes subcrassoides Mills, 1934	11 ± 15	2 ± 4	11.65*
Aethiopella sp.	32 ± 53	3 ± 5	13.10*
Entomobryidae			
Entomobrya californica Schött, 1891	31 ± 51	6 ± 9	5.54*
Lepidocyrtus finus Christiansen & Bellinger, 1980	62 ± 104	3 ± 4	12.59*
L. gr. *lanuginosus* (Gmelin, 1788)	115 ± 192	6 ± 9	12.78*
Seira bipunctata (Packard, 1873)	749 ± 1271	18 ± 30	14.17*
S. dubia Christiansen & Bellinger, 1980	771 ± 1312	22 ± 35	13.65*
S. purpurea (Schött, 1891)	1118 ± 1918	18 ± 29	13.89*
Paronellidae			
Salina banksi MacGillivray, 1894	31 420 ± 53 677	253 ± 487	14.90*
Katiannidae			
Sminthurinus ca. *radiculus* Maynard	32 ± 51	7 ± 3	11.34*
S. ca. *conchyliatus* Snider	20 ± 32	5 ± 2	10.34*
S. ca. *latimaculosus* Maynard	35 ± 57	5 ± 5	11.51*
Sminthurididae			
Sphaeridia pumilis (Krausbauer, 1898)	27 ± 46	6 ± 2	8.15*
Sminthuridae			
Sphyrotecha ca. *mucroserrata* Snider	35 ± 58	3 ± 3	11.82*
Bourletiellidae			
Deuterosminthurus maassius Palacios-Vargas & González, 1995	304 ± 507	15 ± 26	14.01*

SD, standard deviation.

[a] Degrees of freedom = 5.

*$p < 0.05$.

the rainy season with 925 438 specimens collected. However, its abundance decreased during the dry season, and only 983 individuals (65% of the total number of individuals) were collected at this time. Other species exhibited similar seasonal changes, decreasing considerably during the dry season (Fig. 15.2). Results of t-tests indicated significant differences between rainy and dry seasons for the abundance of total Collembola ($t = 2.17$, degrees of freedom (d.f.) $= 131$, $p = 0.03$), and for each species (Table 15.1). In contrast, the Shannon diversity index had higher values during the dry season than during the rainy season ($H' = 1.56$ and 0.52, respectively).

During the dry season, many arthropod groups migrate vertically from soil to canopy to encounter more suitable conditions of humidity and temperature. The

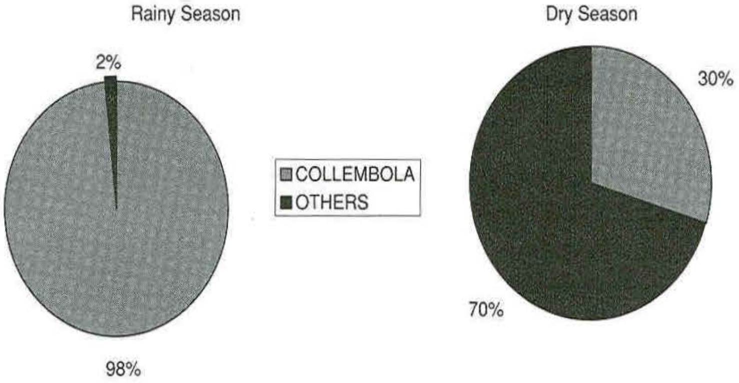


Fig. 15.1. Percentage of Collembola and other arthropods in the Chamela canopy during the rainy and dry seasons.

canopy at Chamela supports many epiphytic plants, such as *Tillandsia* spp. (Bromeliaceae), that provide a shelter from extreme climatic conditions. Eleven genera collected in the canopy at Chamela have been reported living in *Tillandsia* spp. elsewhere (Palacios-Vargas, 1981), and 12 species were collected both in the canopy and soil at Chamela (Palacios-Vargas & Gómez-Anaya, 1993). These vertical migrations and the lack of predators explain why species diversity of Collembola increases notably in the canopy during the dry season.

Assemblage composition of tropical rainforest at Chajul

In the canopy of the Chajul tropical rainforest, 26 species of Collembola were collected (Table 15.2). Of the

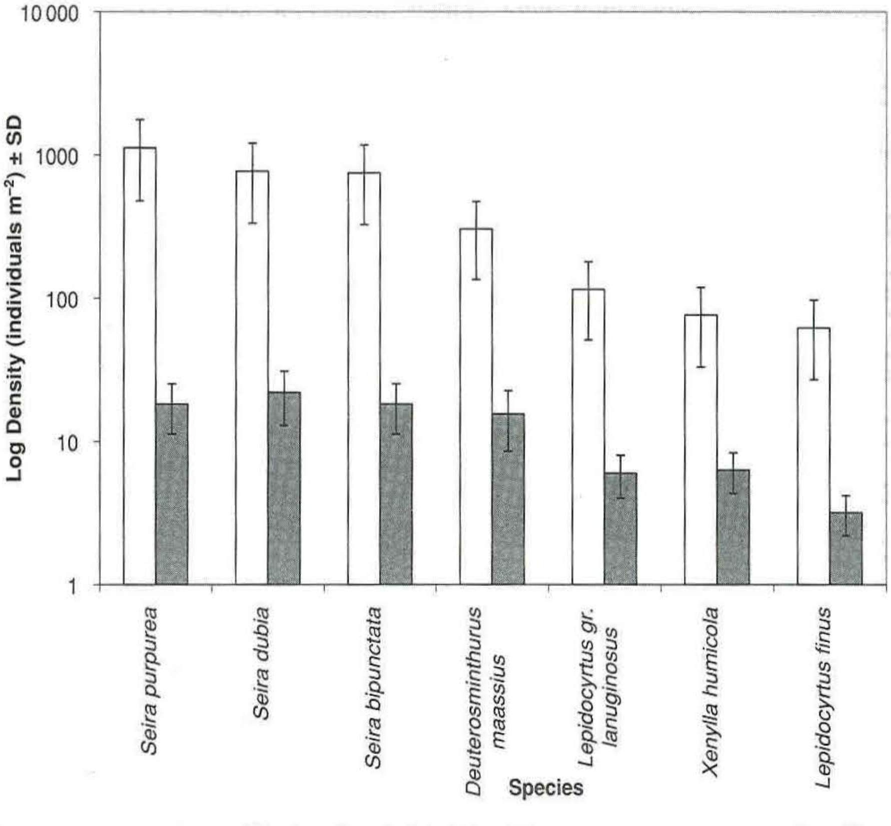


Fig. 15.2. Logarithm of seasonal density and standard deviation of the most abundant Collembola species at Chamela, during the wet (open bars) and dry (closed bars) seasons.

Table 15.2. *Collembola collected from the canopy at Chajul, Chiapas, Mexico*

Taxa	Species
Odontellidae	*Superodontella sp.*
Brachystomellidae	*Brachystomella surendrai* Goto, 1961
Neanuridae	*Arlesia sp.*; *Pseudachorutes indiana* Christiansen & Bellinger, 1980; *Neotropiella sp.*
Isotomidae	*Folsomides angularis* (Axelson, 1905); *Proisotoma sp.*
Entomobryidae	*Seira purpurea* (Schött, 1891); *Lepidocyrtus* ca. *finus*; *Willowsia sp.*; *Psudosinella sp.*; *Entomobrya sp.*; *Americabrya sp.*;
Sminthurididae	*Sphaeridia sp.*
Katiannidae	*Sminthurinus latimaculosus* Maynard, 1951; *Sminthurinus quadrimaculatus* (Ryder, 1878)
Sminthuridae	*Sphyrotheca mucroserrata* Snider, 1978; *Sminthurus sp.*;
Dicyrtomidae	*Calvatomina sp.*; *Dicyrtoma sp.*; *Ptenothrix sp.*;
Paronellidae	*Paronella sp.*; *Campylothorax sp.*; *Salina banksi* MacGillivray, 1894
Bourletiellidae	*Deuterosminthurus* ca. *tristani*; *Bourletiella sp.*

6644 arthropods (338 individuals m^{-2}) collected in the two fumigations of 1994 (3208) and 1995 (3436), 581 (30 individuals m^{-2}), 9% of the total number of arthropods, were springtails. This included 275 individuals (28 individuals m^{-2}) in 1994 and 306 individuals (31 individuals m^{-2}) in 1995 (Fig. 15.3). No significant differences were found between the two studied years ($t = 0.14$, d.f. $= 6$, $p = 0.09$) and the abundance of Collembola appears to be more or less constant across years in this forest.

The most abundant species in both samples at Chajul was *Deuterosminthurus* ca. *tristani*, followed by *S. banksi*. This situation is the opposite to that in the dry forest of Chamela, where *S. banksi* dominated and *Deuterosminthurus maassius* Palacios-Vargas & González ranked fifth in abundance during the rainy season. The Shannon diversity index recorded in July 1995 at Chajul was higher than that observed in Chamela ($H' = 2.03$, $J' = 0.69$, where J' is Pielou's evenness index), and species diversity differed significantly between the two localities ($t = 18.37$, $p < 0.05$).

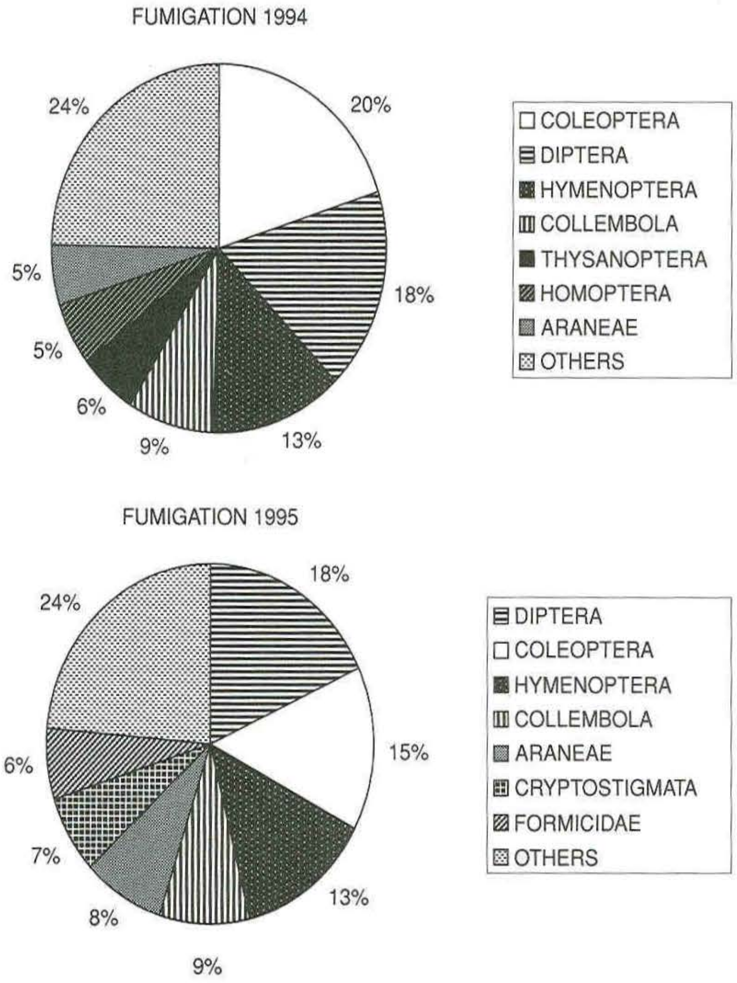
Assemblage composition in temperate forests

In temperate forests, populations of canopy Collembola are significantly lower than in tropical zones. When fogging various oak species in three distinct locations in the Mexico Valley, Tovar (1999) observed that Collembola constituted 32.5% of all arthropods in epiphytic habitats during the rainy season, whereas in the dry season they made up only 8.5% of the total number of individuals. Acari were the dominant group in abundance in these locations (Fig. 15.4).

Samples obtained from *Tillandsia* spp. in the states of Morelos (Chichinautzin) and Hidalgo (El Chico) yielded a total of 36 species (Table 15.3). The most abundant species were *Pseudisotoma sensibilis* Tullgerg in Chichinautzin and *S. quadrimaculatus* (Ryder) in El Chico. However, *S. quadrimaculatus* was the most abundant species during the rainy season in both states, and it decreased significantly in abundance during the dry season. Nevertheless, in Morelos, the abundance of Collembola was higher during the dry season than during the wet season. Diversity increased during the rainy season, and abundance of *P. sensibilis* decreased (H'dry season $= 0.46$; H'rainy season $= 1.8$). During the rainy season, the Shannon diversity index was significantly higher in Chichinautzin than in El Chico (Table 15.4; $t = 64.85$, $p < 0.05$).

Differences between temperate and tropical forests

The assemblage structure of Collembola differs between temperate and tropical forests. In particular, the Paronellidae are frequent in tropical forests but not in the temperate forests of the Mexico Valley. Clusters of collembolan genera collected by fogging in Chamela and



FUMIGATION 1994

FUMIGATION 1995

Fig. 15.3. Relative abundance of the most abundant arthropod groups in the canopy of the rain forest in Chajul, for samples obtained in 1994 and 1995.

Chajul showed greater similarity than did those collected in the epiphytic bromeliads of *Tillandsia* spp. collected on the Chichinautzin lava flow and in El Chico National Park (Fig. 15.5). This suggests a great habitat variety in the canopy and in the diversity of habitats offered by epiphytes occupied by specialized sets of arthropod. Table 15.4 details values of species diversity for all localities. Comparisons of the Shannon diversity index between Chamela and Chichinautzin show significant differences ($t = 48.48$, $p < 0.05$) as did that for Chamela with El Chico ($t = 142.06$, $p < 0.05$). The same comparison between Chajul with Chichinautzin and with El Chico also yielded significant differences ($t = 6.85$, $p < 0.05$ and $t = 10.79$, $p < 0.05$, respectively). A significant effect of vegetation type on springtail density was detected by ANOVA ($F = 4.31$, d.f. = 2,108, $p = 0.02$), and Tukey's test emphasized differences between epiphytes and rainy forest (Chajul, $p = 0.04$).

The sets of Collembola collected in the canopies of El Chico and Chichinautzin were more similar than those collected at Chamela and Chajul. The two last localities were faunistically very different, with only one species in common between the tropical dry forest and the tropical rainforest. When we compared similarities in species composition, assemblages of Collembola living inside the epiphytic *Tillandsia* at the two localities in Central Mexico were more similar than those living in the canopy and obtained by fogging. Nevertheless, there was a clear difference in the number of species and their abundance in *Tillandsia* in both localities. At the Chichinautzin lava flow, there were 18 species, whereas 23 species were present at El Chico. Among those present at the first locality, *P. sensibilis* was the most

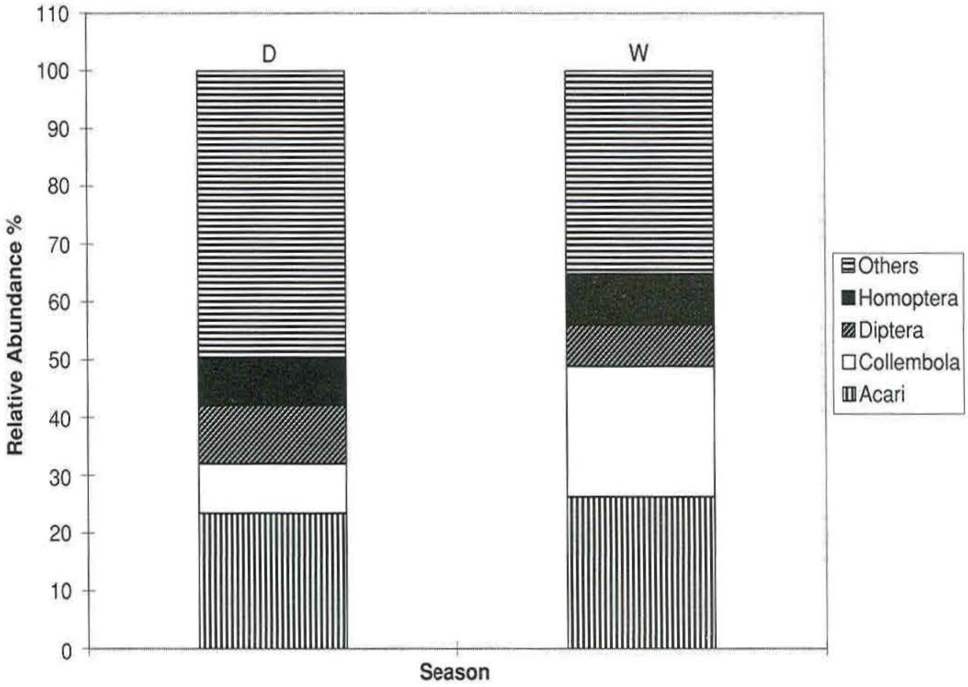


Fig. 15.4. Percentage of individuals collected in a *Quercus* spp. forest during the dry (D) and wet (W) seasons, detailed for the most common arthropod orders (modified from Tovar, 1999).

abundant. This species was also present during the rainy season but less abundantly. It is interesting to note that most of the species at Chichinautzin were more abundant during the dry season, with the exceptions of *Seira* sp., *S. quadrimaculatus* and *Sminthurus* sp. At El Chico during the rainy season, the most abundant species were *S. quadrimaculatus*, *Schoettella distincta* (Denis) and *Sphaeridia* gr. *brevilipa*. Species diversity was high during the dry season in Chichinautzin.

In contrast, at Chamela Biological Station, most species were better represented and more abundant during the rainy season. Here, the most abundant species were *S. banksi*, *D. maassius*, *Seira* spp., *Lepidocyrtus* sp., *Xenylla humicola* (Fabricius) and *Ceratophysella gibbosa* (Bagnall). Collembola were much more abundant during the rainy season, mainly in September, when they reached densities of about 3 million specimens per 100 m^2. Shannon–Weaver diversity, in contrast, was highest during the dry season.

Seasonality of Collembola

Seasonality is an important factor that determines the structure of collembolan assemblages in each forest. Despite different sampling methods being used in each locality, seasonal variation was detected and these differences were significant. Therefore, composition and abundance were significantly affected by seasonal factors.

Most species were more abundant during the rainy season in all the Mexican forest canopies studied and in the epiphytic *Tillandsia*. At Chamela, remarkably, *S. banksi* can reach populations of several millions in 1 ha. The temperate forest in middle Mexico (Hidalgo and Morelos States) includes a characteristic species during the rainy season – *S. quadrimaculatus* – whereas *P. sensibilis* is the most abundant species during winter (dry season).

The extraordinary abundance of *S. banksi* can probably be explained by the high level of humidity and the amount of organic debris in the canopy, which represents 75% of the canopy's vegetable matter (Martínez-Yrizar *et al.*, 1996). It may reflect the feeding habits of this species in the canopy – both detritivorous and mycetophagous – and the reduced numbers of predators in this environment.

Soil and litter are the primordial habitats of springtails. Nevertheless, a rich and very abundant fauna has been collected by insecticide knockdown in trees

Table 15.3. *Seasonal abundance of Collembola associated with* Tillandsia *spp. from Chichinautzin (Morelos State, abundance by plant), and El Chico National Park (Hidalgo State, abundance by 120 plants)*

Taxa	Chichinautzin lava flow			El Chico National Park rainy season
	Dry season	Rainy season	*t* value[a]	
Hypogastruridae				
Ceratophysella denticulata (Bagnall, 1941)	–	2	–	–
Ceratophysella succinea (Gisin, 1949)	–	–	–	20
Schoettella distincta (Denis, 1931)	–	–	–	3736
Xenylla grisea Axelson, 1900	–	–	–	879
X. proxima Denis, 1931	5	11	11.13*	–
Brachystomellidae				
Brachystomella barrerai Palacios-Vargas & Najt, 1981	4	1	5.33*	–
Neanuridae				
Friesea hoffmannorum Palacios-Vargas, 1982	44	34	5.92*	26
F. claviseta Axelson, 1900	–	–	–	1
F. sublimis Macnamara, 1921	52	13	2.29*	–
Pseudachorutes subcrassoides Mills, 1934	–	–	–	294
P. corticicolus (Schäffer, 1897)	–	–	–	24
P. boerneri Schött, 1902	45	16	5.53*	–
P. aureofasciatus (MacGillivray, 1893)	–	2	–	–
Onychiuridae				
Mesaphorura sp.	–	–	–	2
Isotomidae				
Folsomides angularis (Axelson, 1905)	–	5	–	24
Proisotoma ca. frisoni	–	–	–	63
Isotoma anglicana Lubbock, 1862	–	–	–	100
Pseudisotoma sensibilis (Tullgerg, 1876)	5099	316	5.89*	74
Cryptopygus sp.	–	–	–	3
Entomobryidae				
Entomobrya suzannae Schött, 1942	–	–	–	227
Americabrya arida (Christiansen & Bellinger, 1980)	11	68	3.34*	–
Seira sp.	53	93	11.78*	–
S. purpurea (Schött, 1891)	–	–	–	460
Pseudosinella ca. *fallax*	2	–	–	–
Pseudosinella sp.	–	–	–	128
Lepidocyrtus finensis Maynard, 1951	6	7	0.39	–
L. finus Christiansen & Bellinger, 1980	4	3	0.37	131
Willowsia sp.	–	–	–	–
Sminthurididae				
Sphaeridia sp.	55	18	1.99*	1760

(*cont.*)

Table 15.3. (*cont.*)

Taxa	Chichinautzin lava flow			El Chico National Park rainy season
	Dry season	Rainy season	*t* value[a]	
Katiannidae				
Sminthurinus quadrimaculatus (Ryder, 1878)	58	382	14.72*	14 349
Sminthuridae				
Sminthurus sp.	18	114	16.09*	4
Sphyrotheca confusa Snider, 1978	–	–	–	5
Dicyrtomidae				
Ptenothrix sp.	–	2	–	–
P. marmorata (Packard, 1873)	–	–	–	110
Dicyrtoma hageni (Folsom, 1896)	–	–	–	1

[a] *t* values compare the abundance of species between the dry and rainy seasons in Chichinautzin lava flow.
*$p < 0.05$.

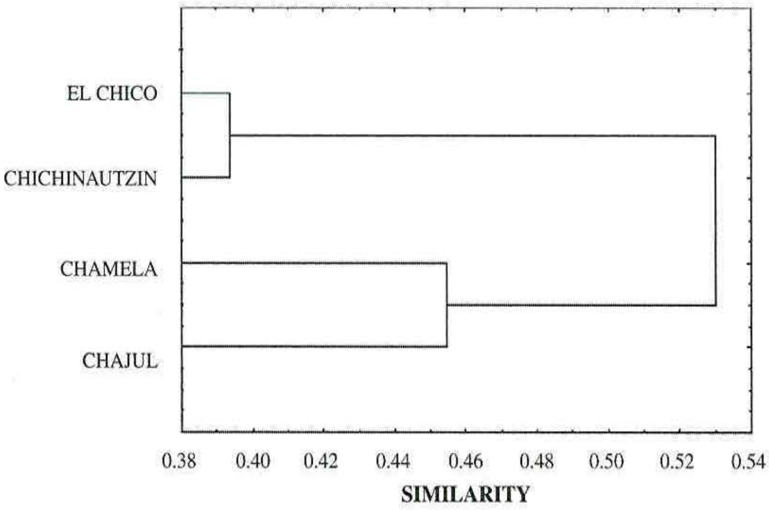


Fig. 15.5. Cluster tree (from unweighted pair-group average analysis) of the genera of Collembola collected in the four types of forest studied.

(Palacios-Vargas *et al.*, 1998, 1999) and from epiphytic plants (Palacios-Vargas, 1981; Palacios-Vargas *et al.*, 2000). Some authors (Watanabe, 1997) have suggested that most arboreal species are members of the soil fauna that have wandered up tree trunks. Despite the lack of specific information about the height on the trees that springtails can reach, we compared data on Collembola from Malaise traps, soil and litter in Chamela. Seven species were shared between Malaise traps and the canopy, but all of them were also collected in soil and litter. Soil and canopy shared three species, and litter shared only two with the canopy. There were eight species present in all vertical sections in the forest. The highest average density of Collembola from the Chamela canopy during the rainy season was represented by epiedaphic species such as *S. banksi* (31 420 ± 53 677 individuals m^{-2}) and *Seira purpurea* (Schött), which usually do not live in the soil or litter. *Seira dubia* Christiansen & Bellinger and *Seira bipunctata* (Packard) were also very abundant in the same place at the same time in the soil and litter.

CONCLUSIONS

By fogging the canopy, we have shown that there are important faunal differences in springtail assemblages that

Table 15.4. *Species richness, Shannon's diversity and Pielou's evenness indices for canopy Collembola at four localities, detailed for both the rainy and the dry seasons*

Diversity index	Chamela		Chajul rainy	El Chico rainy	Chichinatuzin	
	Rainy	Dry			Rainy	Dry
Species richness	19	19	26	23	17	14
Shannon's diversity index	0.52	1.56	2.03	1.27	1.8	0.46
Pielou's evenness index	0.18	0.53	0.69	0.41	0.63	0.17

depend on vegetation type. The most common species of Collembola in Mexican canopies are those of the genera *Salina*, *Seira*, *Sminthurinus*, *Deuterosminthurus*, *Pseudisotoma*, *Schoettella*, *Lepidocyrtus*, *Xenylla*, *Sphaeridia*, *Sphyrotheca* and *Ceratophysella*. Some of them are very mobile and feed on fungi growing between the bark and the trunk of the trees, or on moss and lichens such as *Schoettella*. Less common are species of *Neotropiella*, *Entomobrya*, *Brachystomella*, *Pseudachorutes*, *Americabrya*, *Friesea* and some dicyrtomids. Some taxa may be collected occasionally, such as *Mesaphorura* and *Crytopygus* spp., which are soil specialists.

Differences in the structure of collembolan assemblages from the canopies of tropical and temperate forests are clear. Tropical forests (dry or humid) are characterized by the presence of abundant specimens of *Salina*, which is completely absent from the temperate *Abies–Quercus* forest. The tropical dry forests have a rich diversity of Collembola well adapted to seasonal variations (Palacios-Vargas *et al.*, 1999). In each forest type, the main seasonal differences relate to the relative abundance of species that are, nevertheless, present during both the dry and the wet seasons. This affects significantly measurements of diversity (through changes in evenness values) across seasons.

Comparison between Chajul and Chamela proved very interesting, even though only two foggings were performed at Chajul (July 1994 and July 1995), and seven at Chamela. The number of species collected was very similar (26 and 19, respectively), but the composition and abundance were completely different. The only species that these tropical forest canopies shared was *S. banksi*. The following species were also well represented at Chajul (in decreasing order): *Deuterosminthurus ca. tristani*, *S. banksi* and *Willowsia* sp. At Chamela, the most abundant species in the canopy were *S. banksi*, *S. purpurea*, *S. dubia*, *S. bipunctata*, *D. maassius*, *Lepidocyrtus finus* , *X. humicola*, *Lepidocyrtus finensis* Maynard, *Ceratophysella gibbosa*, *Sphyroteca* ca. *mucroserrata* and *Sminthurinus* ca. *latimaculosos*.

In Chajul, species diversity was the highest of all localities, indicating a high species richness of springtails in tropical rainforests. Evenness was high, too, in contrast to Chamela, where it was low during the rainy season. The results obtained by hand collecting in *Tillandsia* spp. were very different from those collected by fogging, implying that the fauna living in *Tillandsia* is more diverse and more varied in feeding habits than that indicated by fogging.

There are many vegetation types in Mexico, and the structure of springtail assemblages in their canopies can vary substantially. At least for Central Mexico and in tropical dry forests, we now have good information on the genera present. The canopies of tropical rainforests in Mexico, in contrast, require much further investigation.

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